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# NEST-SITE SELECTION BY CAVITY-NESTING BIRDS OF RIPARIAN HABITATS IN IOWA

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Nest-site selection is an important component of habitat selection by birds (Hildén 1965). Nest-sites selected by a species should represent the cumulative effects of evolutionary pressures that have maximized reproductive success (Caccamise 1977). Competition for nest-sites may be rigorous among cavity-nesting species (von Haartman 1957, Franzreb 1976) and may limit the availability of sites suitable for nesting.

Although considerable effort has been expended to study interspecific relationships within avian communities, little research has been devoted to the analysis of nest-site selection at the community level. Beecher (1942) provided a general description of nest-site selection within a community. Preston (1946), Preston and Norris (1947), Cruickshank (1956), Taylor (1965), and DeGraff et al. (1975) have reported on nest heights selected by birds in various habitats, but they did not provide supplemental nest-site measurements. More recently, Conner and Adkisson (1977), studying five woodpecker (Picidae) species, and McCrimmon (1978), studying five heron (Ardeidae) species, have conducted principal component analysis on several nest-site measurements.

In view of the general lack of information on nest-site selection at the community level, particularly for cavity-nesting species, the objective of this paper is to describe the interrelationships among nest-sites chosen by cavity-nesting species of riparian communities (herein defined as uncultivated land within 250 m of the stream edge).

## STUDY AREA AND METHODS

Twenty-eight sites were selected for study in southeastern Guthrie County, Iowa, along Brushy Creek, Beaver Creek, and the Middle and South Raccoon rivers. In choosing study sites, an effort was made to sample a broad spectrum of riparian habitats. A total of 142 ha comprising six general habitat types was sampled. Characteristics of the six types (herbaceous, 8.9 ha; savannah, 5.5 ha; scrub, 3.8 ha; wooded edge, 6.8 ha; floodplain woodland, 28.4 ha; and upland woodland, 88.8 ha) and the study area in general are detailed in Stauffer and Best (1980).

Fieldwork was done mid-April through mid-July in 1976 and 1977 as part of an avian community study (Stauffer and Best 1980). Some nests were found during early morning breeding-bird censuses of the study sites, but most were located after censuses and during evening hours by watching nesting behavior and systematically searching suitable areas. We attempted to locate nests of every cavity-nesting species present on each study site. The sample is biased, however, because nests located in more open sites where birds could be followed more easily were represented disproportionately.

The following measurements were recorded for each cavity nest located: nest height and height of supporting substrate, relative nest height (nest height/support height), limb (trunk) diameter and angle from horizontal at the nest cavity, and compass orientation of the nest-cavity entrance. The date of nest initiation either was determined by direct observation of nest building or was estimated by backdating from the time when young were observed being fed.

Before statistical operations were performed, the data were checked for normality. The variables nest height, support-structure height, and supporting limb (trunk) diameter were found not to be normal and were transformed by using natural logarithms, resulting in more normal distributions. Mean values and Pearson product-moment correlations among the variables were calculated for primary (i.e., cavity-excavating) and secondary cavity nesters. A direct discriminant function analysis (Nie et al. 1975) was used to compare interrelationships of the species' nest-sites on the basis of the measured variables.

## RESULTS AND DISCUSSION

*Univariate analysis.*—In general, nests of primary cavity nesters (PCN) were higher ($\bar{x}$ = 8.3 m) than those of secondary cavity nesters (SCN, $\bar{x}$ = 6.2 m) (Table 1). Nest height differences were statistically significant among PCN and among SCN as well as between the two groups of species (Table 2). Similar trends were evident in support-structure height (Tables 1, 2). Nest and support-structure heights were more variable for SCN than for PCN (as indicated by higher F values, Table 2) and were weakly correlated with the date of nest initiation in the former (Table 3). The greater variation in nest-sites of SCN may be because, as a whole, these species have fewer options in their choice of nest-sites and must choose from those abandoned by PCN or that occur naturally.

Although relative nest height differed significantly among SCN (Table 2), it was quite consistent among PCN. Nests of all cavity nesters, however, were placed relatively lower in tall than in short support structures (Table 3), probably because taller snags (standing dead trees) have smaller limbs on top that are unsuitable for nesting. Shorter snags generally are older and in more advanced stages of decay; consequently, their smaller branches more likely would have been broken off.

Limb (trunk) diameter at the nest cavity differed significantly for all comparisons made (Table 2). PCN selected larger limbs (trunks) for nest support ($\bar{x}$= 26.0 cm) than did SCN ($\bar{x}$= 21.6 cm) (Table 1), suggesting that not all cavities abandoned by PCN are preferred equally by SCN. (Approximately 20–30% of SCN nests were in natural cavities, which, in part, may explain the difference between PCN and SCN nest-sites.) The negative correlation of supporting limb diameter with date of nest initiation for each group (Table 3) probably resulted from Downy Woodpeckers (see Table 1 for scientific names) and House Wrens nesting relatively late in the breeding season. These species selected relatively small-diameter limbs (trunks) for nest support (Table 1).

TABLE 1

MEANS AND STANDARD DEVIATIONS OF SELECTED VARIABLES MEASURED AT 298 CAVITY NESTS

| Species | Sample size | Nest height (m) | Support-structure height (m) | Limb (trunk) diameter at cavity (cm) | Supporting limb (trunk) angle (°)[a] |
|---|---|---|---|---|---|
| Primary cavity nesters | 134 | 8.3 ± 3.7 | 13.6 ± 6.3 | 26.0 ± 10.5 | 69.7 ± 19.6 |
| Common Flicker (*Colaptes auratus*) | 31 | 8.1 ± 3.2 | 14.9 ± 6.6 | 34.5 ± 10.6 | 73.7 ± 17.1 |
| Red-bellied Woodpecker (*Melanerpes carolinus*) | 14 | 8.4 ± 2.7 | 13.6 ± 7.4 | 26.7 ± 5.9 | 63.6 ± 23.1 |
| Red-headed Woodpecker (*M. erythrocephalus*) | 59 | 9.6 ± 3.7 | 14.6 ± 5.7 | 25.7 ± 9.3 | 69.8 ± 18.5 |
| Downy Woodpecker (*Picoides pubescens*) | 30 | 6.1 ± 3.1 | 10.2 ± 5.6 | 18.8 ± 6.0 | 68.0 ± 22.4 |
| Secondary cavity nesters | 164 | 6.2 ± 4.0 | 10.5 ± 7.4 | 21.6 ± 8.9 | 61.3 ± 23.7 |
| Great Crested Flycatcher (*Myiarchus crinitus*) | 13 | 8.5 ± 3.3 | 16.9 ± 7.0 | 24.7 ± 11.1 | 62.7 ± 27.0 |
| Black-capped Chickadee (*Parus atricapillus*) | 25 | 2.2 ± 2.1 | 4.0 ± 5.2 | 20.3 ± 7.8 | 73.6 ± 21.7 |
| White-breasted Nuthatch (*Sitta carolinensis*) | 9 | 7.2 ± 3.1 | 17.8 ± 7.9 | 33.2 ± 13.1 | 55.0 ± 28.1 |
| House Wren (*Troglodytes aedon*) | 82 | 5.4 ± 2.9 | 8.4 ± 5.0 | 19.6 ± 7.1 | 60.8 ± 23.0 |
| Starling (*Sturnus vulgaris*) | 22 | 9.7 ± 4.5 | 15.5 ± 7.8 | 25.9 ± 9.9 | 62.5 ± 16.8 |
| House Sparrow (*Passer domesticus*) | 13 | 10.7 ± 3.8 | 16.4 ± 6.3 | 18.5 ± 5.1 | 39.6 ± 27.2 |

[a] Angle measured from horizontal.

Limb angle at the nest cavity was not different among primary cavity-nesting species (PCNS), but differed significantly among secondary cavity-nesting species (SCNS) and between the two groups (Table 2). The negative correlations of limb angle with nest and support-structure heights for SCN (Table 3) probably is because higher nests were placed in branches that lean more away from the main trunk, whereas lower nests usually were found in snags in advanced stages of decay with only the trunk and the bases of main branches remaining.

Compass orientation of entrances to cavity nests has been found to be nonrandom for several cavity-nesting species (Lawrence 1967, Dennis 1969, Reller 1972, Conner 1975). Nest cavities often are oriented to the south

TABLE 2

F-STATISTICS FROM ONE-WAY ANOVA'S OF DIFFERENCES AMONG SPECIES AND BETWEEN GROUPS OF SPECIES IN THE VARIABLES MEASURED AT CAVITY NESTS

| Variable | All cavity nesters (df = 9, 289) | Primary cavity nesters (df = 3, 130) | Secondary cavity nesters (df = 5, 158) | Primary vs secondary cavity nesters (df = 1, 296) |
|---|---|---|---|---|
| Nest height | 23.66*** | 6.71*** | 26.26*** | 28.15*** |
| Support-structure height | 23.35*** | 6.00*** | 24.92*** | 26.14*** |
| Relative nest height | 2.32* | 1.10 | 3.59** | 0.23 |
| Supporting limb (trunk) diameter | 8.19*** | 10.86*** | 5.63*** | 8.43** |
| Supporting limb (trunk) angle | 3.95*** | 0.96 | 3.86*** | 10.71** |

* $P \leq 0.05$; ** $P \leq 0.01$; and *** $P \leq 0.001$.

and east, which may allow sunlight to warm the nest or permit nest ventilation by prevailing winds (Conner 1975). In our study, there was no consistent pattern in woodpecker nest orientation, although nest orientation was statistically nonrandom for PCN (Table 4). Of the 133 primary cavity nests, 94% were located on the underside of sloping limbs (trunks). Thus, birds may be choosing nest-sites primarily on the basis of limb (trunk) angle, and nest-entrance orientation may be only an indirect consequence of the former (see Conner 1975).

TABLE 3

CORRELATIONS BETWEEN VARIABLES MEASURED AT PRIMARY (N = 134) AND SECONDARY (N = 164) CAVITY NEST-SITES[a]

| Variable | Cavity-nest type | NID | NH | SSH | RNH | SLD | SLA |
|---|---|---|---|---|---|---|---|
| Nest-initiation date | Primary | 1.0 | | | | | |
| | Secondary | 1.0 | | | | | |
| Nest height | Primary | 0.11 | 1.0 | | | | |
| | Secondary | 0.22 | 1.0 | | | | |
| Support-structure height | Primary | 0.11 | 0.70 | 1.0 | | | |
| | Secondary | 0.21 | 0.90 | 1.0 | | | |
| Relative nest height | Primary | −0.01 | 0.29 | −0.46 | 1.0 | | |
| | Secondary | −0.04 | −0.05 | −0.47 | 1.0 | | |
| Supporting limb (trunk) diameter | Primary | −0.16 | 0.10 | −0.01 | 0.07 | 1.0 | |
| | Secondary | −0.28 | 0.05 | 0.12 | −0.21 | 1.0 | |
| Supporting limb (trunk) angle | Primary | −0.15 | 0.09 | −0.02 | 0.14 | 0.38 | 1.0 |
| | Secondary | −0.12 | −0.12 | −0.15 | 0.12 | 0.07 | 1.0 |

[a] Significant ($P \leq 0.05$) correlation values are 0.14 and 0.13 for primary and secondary cavity nest-sites, respectively.

TABLE 4
NEST-ENTRANCE ORIENTATION RELATIVE TO THE CENTER OF THE NEST-SUPPORT STRUCTURE FOR CAVITY-NESTING SPECIES

| | Percent of nests | |
|---|---|---|
| Orientation | Primary cavity nesters | Secondary cavity nesters |
| N | 16 | 14 |
| NE | 9 | 15 |
| E | 20 | 15 |
| SE | 6 | 12 |
| S | 14 | 15 |
| SW | 10 | 8 |
| W | 16 | 10 |
| NW | 9 | 11 |
| Total nests | 133 | 157 |
| Chi-square value | 16.1 | 6.5 |
| Significance level | <0.05 | >0.50 |

On the basis of similarities in woodpecker and Eastern Bluebird (*Sialia sialis*) nest-entrance orientation, Pinkowski (1976) concluded that bluebirds randomly selected nest-sites, most of which were woodpecker cavities. Nest-entrance orientation in our study did not differ between PCN

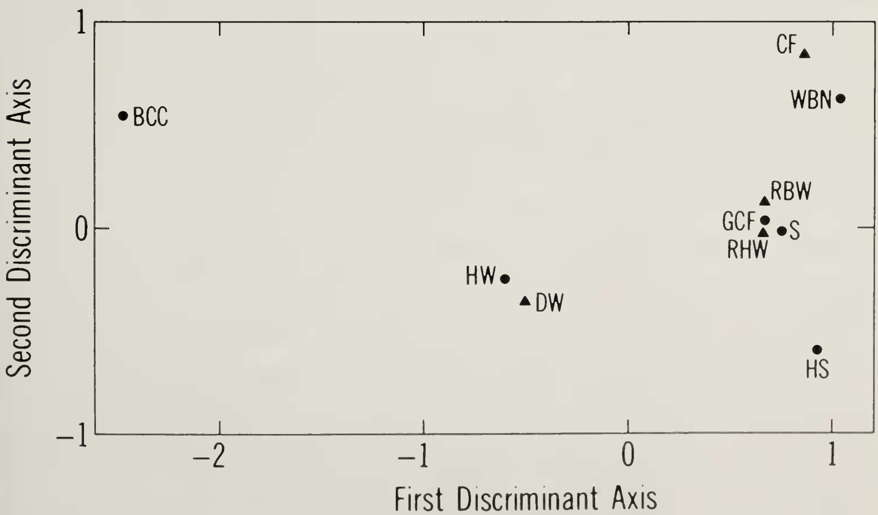


FIG. 1. Two dimensional ordination for nest-sites of 10 cavity-nesting species using the first and second discriminant axes. Species' codes are in Table 1.

and SCN ($\chi^2$ = 8.99, df = 7, $P > 0.10$), seemingly supporting the notion that nest-site selection by SCN is random. Significant differences between PCN and SCN in four of five nest-site measurements, however, suggest that SCN may not randomly select woodpecker cavities even though orientation of the nest-cavity entrances is similar. The apparent paradox may be explained by the fact that snags are continually decomposing; thus, characteristics of a nest-site excavated by a woodpecker may change by the time that the same site is used by a SCN.

*Multivariate analysis.*—To determine the degree of dissimilarity among nest-sites of the 10 cavity-nesting species, a discriminant analysis was conducted using five variables (Table 5). (This was done after the results from a MANOVA of the five variables proved statistically significant.) The species' mean discriminant values then were ordinated on the first two discriminant axes (Fig. 1). Support-structure height loaded most heavily in the first function derived (Table 5). The ordination of nest-sites on the first axis separated only three species (Black-capped Chickadee, House Wren, and Downy Woodpecker) from the others (Fig. 1); all three species chose smaller trees or snags for nesting. The second function further discriminated species primarily on the basis of nest height and supporting limb (trunk) diameter. Values along the resultant axis (Fig. 1) increase as nest height decreases and as supporting limb (trunk) diameter increases. White-breasted Nuthatches and Common Flickers, which nested low in larger structures, and House Sparrows, which nested high in smaller structures, were well separated from the main group on the second axis.

Starlings, Great Crested Flycatchers, and Red-headed and Red-bellied woodpeckers chose notably similar nest-sites on the basis of the five variables used (Fig. 1). This suggests a potential for considerable nest-site competition among these four species, although including additional variables in the analysis might have resulted in better separation. Great Crested Flycatchers nest more often in dead limbs of live trees and in live trees than do the other three species (Stauffer and Best 1980). Thus, although flycatchers select nest-sites structurally similar to those of the other species, the potential for competition may be low. Although Red-headed and Red-bellied woodpeckers choose similar nest-sites, they may avoid competition by selecting different habitats and (or) nesting at different times (Jackson 1976). Starlings have an extended breeding season (Collins and de Vos 1966) and occupy a variety of habitats; thus, they are potential competitors for nest-sites with the other three species (see also Erskine and McLaren 1976, Troetschler 1976, Short 1979). Once, two Starlings were observed taking over an active Red-headed Woodpecker nest.

PCN and SCN were discriminated principally on the basis of support-structure height (Table 5). The other four variables were relatively unim-

TABLE 5

SUMMARY OF DIRECT DISCRIMINANT ANALYSES CONDUCTED ON NEST-SITES OF CAVITY-NESTING SPECIES[a]

| Variable | Standardized coefficients of the first two functions[b] | | | | | | |
|---|---|---|---|---|---|---|---|
| | All cavity nesters | | Primary cavity nesters | | Secondary cavity nesters | | Primary vs. secondary cavity nesters |
| | I | II | I | II | I | II | I[c] |
| Nest height | −0.127 | −0.660 | −2.379 | −1.306 | 1.566 | −1.064 | −0.658 |
| Support-structure height | 1.194 | 0.414 | 3.305 | 2.023 | −0.722 | 1.398 | 1.634 |
| Relative nest height | 0.457 | 0.004 | 2.243 | 1.924 | −0.608 | 1.220 | 0.671 |
| Supporting limb (trunk) diameter | 0.445 | 0.717 | 0.976 | −0.491 | 0.305 | −0.646 | 0.291 |
| Supporting limb (trunk) angle | −0.205 | 0.447 | −0.264 | −0.083 | −0.265 | −0.507 | 0.466 |
| Cumulative variance accounted for | 72.9 | 88.1 | 81.1 | 96.5 | 76.8 | 91.2 | 100.00 |

[a] Analyses were run among all cavity-nesting species, among primary cavity-nesting species, among secondary cavity-nesting species, and between primary and secondary cavity nesters.
[b] All functions presented are significant ($P < 0.05$), as determined by minimization of Wilk's lambda.
[c] Only one function can be derived when only two groupings are being discriminated.

portant in distinguishing between the two guilds. Significant discrimination between the two guilds on the basis of five variables indicates that SCN have selective preferences among the available cavities abandoned by woodpeckers.

The first discriminant function of an analysis among PCNS weighted heavily on support-structure height and somewhat less on nest and relative nest heights (Table 5). (Because relative positions of both PCNS and SCNS when plotted separately on their first two discriminant axes were similar to those in Fig. 1, they are not presented here.) The second function further separated PCNS that were similar for the first function on the basis of support-structure height and relative nest height. Thus, PCNS seem to be partitioning nest-sites mainly on the basis of substrate structure size. Conner and Adkisson (1977), using principal component analysis, were able to define a gradient for nest-sites of five woodpecker species on the basis of nest-tree diameter.

The most important variable derived in the first function that discriminated among SCNS was nest height (Table 5). The second function was dominated by support-structure and relative nest heights. Except for Starlings and Great Crested Flycatchers, the discriminant analysis separated SCNS well.

Patterns of nest-site selection for PCN and SCN differ. Woodpeckers partition nest-sites primarily on the basis of substrate height, whereas SCN mainly choose nest-sites on the basis of cavity height and secondarily by support-structure height.

## SUMMARY

Nest-site selection by 10 cavity-nesting species was analyzed on the basis of five nest-site variables. Discriminant analysis showed considerable separation among nest-sites for 6 of the 10 species, mainly on the basis of nest substrate size. The other four species potentially compete for nest-sites. When analyzed separately, primary cavity nesters and secondary cavity nesters exhibited different patterns in nest-site partitioning. Woodpecker species chose different nest-sites mainly on the basis of support-structure height, whereas secondary cavity nesters primarily segregated nest-sites on the basis of cavity height.

Differences in four of the five variables and results of discriminant analysis suggest that SCN were not randomly choosing cavities abandoned by woodpeckers.

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